Evolutionary Trends in *Cryptocercus punctulatus* (Blattaria: Cryptocercidae)

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Abstract: First instar nymphs of *Cryptocercus punctulatus* are eyeless. The reduced eyes of adults may result from the morphogenetic process of retardation. The blind condition of the youngest nymphs is an adaptation to life in rotting logs and perhaps also represents a preadaptation to life in the termite niche present in a common ancestor of *Cryptocercus* and the termites. The over-all resemblance between first instar nymphs of *C. punctulaus* and termites suggests the neotenic origin of the latter from a blattarian ancestor.

Cockroach systematists have virtually ignored nymphal characters in classifications of the Blattaria. The most widely accepted taxonomic scheme (McKittrick, 1964), is based on adult characters, mostly those of the genitalia. In a recent numerical taxonomic study of adult and nymphal cockroaches, Huber (1974) used a wide range of external morphological characters including many which are ontogenetically homologous in all instars. This enabled him to construct and compare classifications based entirely on nymphal characters with classifications based on adult characters. The nymphal stages produced classifications which were congruent with those of McKittrick (1964) and although obviously diagnostic characters were not found in the nymphs, familial and subfamilial divisions could be detected.

During his study, Huber (1974) made the surprising discovery that, unlike other Blattaria, the first instar nymphs of *Cryptocercus punctulatus* Scudder lack compound eyes. Since this species is regarded by McKittrick (1964, 1965) as the most primitive living cockroach, its phenetic placement in phenograms and centroid component models (Huber, 1974) was of particular interest. Apparently, the eyeless condition did not have much effect on the position of *C. punctulatus* in the classifications of the small nymphs. The eyes of adult *C. punctulatus* are reduced in size compared with other species of cockroaches (Crampton, 1932; Beier, 1974, Fig. 15). Are its eyes smaller because they have had fewer instars in which to grow? Mackerras (1967) refers to various

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other species of cockroaches in which the eyes are reduced or absent. Nothing is known about the ontogeny of eye development in these troglobiont forms. De Beer (1958) proposed the concept of *retardation* as one explanation for the reduction of an adult structure. Perhaps the reduced eyes of *C. punctulatus* are a product of such a process.

The Isoptera are thought to have evolved from Blattaria (McKittrick, 1964; Tillyard, 1936; Brosut, 1973; Emerson, 1961; Rau, 1941). The literature has been surveyed by Wilson (1971:103). Thus, it is interesting to note that early instars of termites also lack compound eyes (Weesner, 1969). The development of compound eyes has been histologically investigated in some of the termites (reviewed by Richard, 1969). In second instar *Cryptocercus*, the eye appears as a small (one-third the size of the antennal socket) and poorly pigmented (reddish-brown) structure. During eye development in the termites (Richard, 1969:179), a reddish-brown pigment appears in the seventh stage. The eye later darkens to a deep brown in both termites and in *C. punctulatus*. A comparative study of eye ontogeny in *Cryptocercus* and the termites would be profitable.

Although *Cryptocercus* is regarded as primitive among cockroaches, it nevertheless possesses many unusual, even unique, characters. Winglessness, subsocial life, the presence of flagellates in the gut for the digestion of cellulose and the structure of the proventriculus of *C. punctulatus* are all adaptations for life in rotting logs and for xylophagy. The blindness of the first instar and the reduced condition of the eye in later instars could be added to this list. All of these features may be regarded as adaptations to life in the termite niche. Perhaps these were present as preadaptations in a common ancestor of *Cryptocercus* and termites. First instar *C. punctulatus* moreover bear a remarkable, even startling, resemblance in size, shape and appearance to many termites (e.g., *Reticulitermes* sp.) (Cleveland et al., 1934). Perhaps in such cockroaches (except for winglessness), we have a plausible model of the blattarian ancestor of the Isoptera.

It is possible to speculate on the mode of evolution which produced the termites. Neoteny seems to have been a significant process during orthopteroid evolution (reviewed by Huber, 1974). Richard (1969) notes that adult termite ommatidia possess many embryonic characters. This fact together with the similarities mentioned above strongly suggests a neotenic derivation of the Isoptera from a *Cryptocercus*-like cockroach ancestor. A numerical phenetic study of suitably chosen termites and nymphal cockroaches should yield new insights into the relationships between these groups.

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BOOK REVIEW

Insect Hormones. V. J. A. Novak. Second English Edition. 600 pp. Chapman & Hall, London; Halsted Press; John Wiley & Sons, New York. $49.50. 1975.

Rarely does a textbook fulfill a real need, rather than just increase the rapidly growing literature. Novak's book is one of these welcome, rare contributions. It is actually the English translation of his 4th edition which appeared in Czech, and it is in many ways a remarkable treatese. It deals briefly with the history of insect endocrinology, then describes the techniques used in research, including tissue and organ culture. Ecdysone, the juvenile hormone, and the corpora cardiaca hormones are described in the 3rd chapter on 120 pages. This is followed by a discussion of natural and synthetic substances with hormone activity. The role of hormones in morphogenesis and diapause, the neurohormones, protohormones, exohormones, and the substances with allegedly hormonal characteristics occupy 100 pages. A separate chapter is devoted to the effects of insect hormones on noninsects. The book concludes with a stimulating discussion about the theoretical and practical significance of insect hormones. There is an extensive list of references, a good subject index and an author index. This is a remarkable and valuable book, very useful as a reference, amply documented, that can be considered a major and unique addition to the literature on invertebrate endocrinology. Novak's book will remain an important summary of the subject for years to come for all who are working with insect endocrinology.

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